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BIOLOGY AND METAMORPHOSIS OF SOME SOLOMON ISLANDS DIPTERA. PART II: SOLVA BERGI JAMES (ERINNIDAE), WITH A COMPARISON OF RELATED SPECIES*

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The general introduction to a proposed series of papers on biology and metamorphosis of some Diptera reared in the Solomon Islands during World War II is given in a previous paper (Berg, 1947). This second paper of the series concerns a species of Erinnidae, *Solva bergi*, recently described by Dr. Maurice T. James (1951) from specimens collected and reared by the author.

I am indebted to Dr. James, of Washington State College, for preparing the original description of *S. bergi.* Four larvae and puparia of *S. pallipes* (Loew), which proved valuable for comparative studies, were furnished by Dr. Alvah Peterson, of Ohio State University. A grant-in-aid from Ohio Wesleyan University enabled me to employ Mr. C. R. Roelofs, Jr., student at Ohio Wesleyan, who gave excellent assistance in the preparation of illustrations.

To ensure accuracy of proportions, tracings of micro-projector images were used as bases of all drawings. Larvae, puparia, pupae and adults of *S. bergi* are deposited at the United States National Museum for the convenience of future investigators.

Adults of *Solva bergi* were frequently observed resting on leaves of jungle undergrowth near the Tenaru River about one and one-half miles from the north coast of Guadalcanal. Their conspicuous black and yellow coloring and their habit of resting on the upper surfaces of leaves render them easily seen. All were in moist, shaded situations. Although they often flew when disturbed, they were captured readily in a net, and ten females and five males were collected in this way from September through December, 1944. Mating, oviposition and food habits of the adults were not observed.

On April 11, 1945, more than sixty larvae of this species were found in the moist, spongy, fermenting bark of a branch lying on the bank of the Tenaru River about two miles from its mouth. A

^{*} Based upon rearing and biological observations made on Guadalcanal Island during 1944 and 1945, while on active duty in a Malaria Control unit of the United States Navy. The statements and opinions set forth are the author's and not necessarily those of the Navy Department.

variety of dipterous larvae lived in this sour smelling bark, feeding on it, on the fungus which it supported or on other larvae living in this material. Malloch, who found the larvae of *S. pallipes* under similar conditions, wrote (1917:342), "The Xylomyia [*S. pallipes*] larvae were found to be predaceous, feeding indiscriminately upon the other larvae." While it seems likely that larvae of *S. bergi* are also predaceous, observations in support of this suggestion are lacking. Other flies reared from this collection represent the families Chloropidae, Dolichopodidae, Mycetophilidae, Neriidae, Psychodidae, Stratiomyidae (four species) and Syrphidae.

The pulpy bark became progressively more liquid and more malodorous as it continued to ferment and decompose in the laboratory. It was finally reduced to a mass of dissociated fibers suspended in a thick, dark brown liquid, which was frequently decanted off to avoid the possibility of toxic effects upon, or asphyxiation of, the larvae.

Larvae of S. bergi move about relatively little. They made no attempt to leave the culture medium before pupation. Pupation occurs within the puparium (fig. 7), the leathery integument of the last stage larva, which undergoes no conspicuous change in shape such as that observed during formation of the puparia of Cyclorrhapha. Two or three days after cessation of larval movement, the outline of the pupa can be seen when light is transmitted through the puparium. A specimen thus observed as a pupa within the puparium on April 25 emerged as an adult seven days later.

Before emergence, each puparium splits along the mid-dorsal line throughout the mesothoracic, metathoracic and first abdominal segments, and more than half way back through the second abdominal segment (fig. 1). A transverse cleft between dorsal surfaces of the prothorax and mesothorax intersects the longitudinal slit and in some specimens extends around on the ventral side, detaching head and prothorax from the rest of the puparium¹.

The pupa works its way forward and upward through the longitudinal emergence slit until the head, thorax and first four abdominal segments are out of the puparium. Usually it stops in this position, with fifth abdominal segment in the emergence slit and sixth and seventh segments still within the puparium. This pupal

¹ It is evident from the description that the single specimen from which Townsend described the **S. pallipes** puparium (1893:164) lacked not only the head, as he stated, but also the prothoracic segment.

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integument ruptures dorsally to produce a Y-shaped opening across the head and thorax, and the adult emerges, leaving the pupal exuvia loosely clasped in the puparium (fig. 6). A few pupae emerge completely from the puparium before yielding the adult fly (fig. 8).

Emergence requires several minutes. The emergence slit was noticed in a puparium at 11:20 a.m. At 11:25, the pupa was wriggling out. There were intervals of slow to moderate activity and intervals of rest. By 11:35, all but the last three segments of the pupa had emerged. Although it continued to move at intervals for the next ten minutes, it made no further progress. After an interruption of one hour in my observations, I found the adult fly emerged and active. The pupal exuvia was completely free from the puparium.

Twenty-four males and 35 females were reared from the collection made on April 11. Emergence began with a single specimen on April 30 and rapidly rose to a peak of 16 specimens on May 5.

A few additional specimens of *S. bergi* were reared from larvae found beneath moist bark of a fallen tree on April 19, 1945. This collection was also made on the bank of the Tenaru River, about one-half mile downstream from the April 11 collection, and the *S. bergi* larvae were again associated with larvae of several other species.

Description of Puparium

The known larvae of Solva and Xylomyia (as recognized by Steyskal, 1947) are broad and flat, distinctly segmented, composed of head, three thoracic and eight abdominal segments. They differ markedly from the elongate, subcylindrical, soft-bodied larvae of Erinna (= Xylophagus) and other genera of Erinnidae, but they resemble Stratiomyidae larvae very closely. Like them, larvae of Solva and Xylomyia have leathery, thick integuments, which effervesce strongly when placed in dilute hydrochloric acid, apparently because they are covered or inlaid with calcareous bodies are flat, superficial plates, in contrast to the nail-shaped processes of Stratiomyidae larvae. Considering larval characteristics, it is not at all strange that many investigators have regarded the species now referred to Solva and Xylomyia as constituting a sub-family of Stratiomyidae³.

²Such treatment with a dilute acid is an important step in cleaning these puparia before mounting them for study.

The problem of identifying larvae of these two genera is primarily one of distinguishing them from Stratiomyidae larvae and from each other. In order to determine which of the anatomical features observed in S. bergi occur also in other species of Solva, comparisons were made throughout this study with larvae and puparia of S. pallipes (Loew). Published descriptions and figures of larvae of three other species of Solva and Xylomyia were used in attempting to select characters which they possess in common and which distinguish them from all Stratiomyidae larvae. These species are Solva marginata Meigen, Xylomyia maculata (Meigen) and X. varia (Meigen).

Since the integument of the last stage larva is not altered in shape when pupation occurs within it, and since emergence finally leaves this integument more clear and more easily studied than is the larva, most descriptions of *Solva* and *Xylomyia* larvae are based upon this empty larval skin or puparium.

The puparium of S. bergi (fig. 7) measures $2.0-2.8 \times 7.4$ -9.2 mm. The larval integument is inlaid with small plates or scales which give it an appearance not unlike that of pebbled leather (fig. 9). Some of these scales are distinctly darker than others, and the pigmented ones are distributed in patterns which are fairly constant and characteristic (figs. 1, 2, 3).

Conspicuous smooth, clear areas, in which the small scales and the reticulated, shagreened appearance of the integument produced by them do not occur, are found on both prothorax and mesothorax of *S. bergi*. Single, large, median clear areas occur on dorsal surfaces of both segments (fig. 1), while on the ventral surfaces three clear areas are found on the prothorax, and two on the mesothorax (fig. 2).

Malloch (1917:317), who regarded the "Xylomyiinae" as a subfamily in Stratiomyidae, used: "Thoracic segments 1 and 2 each with a smooth plate on dorsum," as a key character to distinguish these larvae from those of other subfamilies of Stratiomyidae. Unfortunately, he confused this situation by mentioning in his

⁸Although Séguy (1926: 81) placed these species in Erinnidae, he divided this family into Xylomyiinae, all known larvae of which are the flat, stiff-bodied type herein discussed, and Erinninae, larvae of which have elongated, subcylindrical bodies covered with thin, flexible integuments. This division, based upon adult characters, tends to support the conclusion inevitably reached by students of life cycles and immature stages, that the family Erinnidae includes two remotely separated phylogenetic groups.

description of S. pallipes (p. 342), "a pair of narrow transverse plates on dorsum of metathorax," where he undoubtedly meant to write, "mesothorax." As illustrated by Peterson (1951: fig. D 13: B), the paired, transverse clear areas on dorsum of mesothorax of S. pallipes almost touch each other at the mid-dorsal line. In addition, S. pallipes larvae have single, median clear areas on both dorsum and venter of the prothorax, but none occur on the metathorax nor on venter of mesothorax.

Although the failure of European authors to mention anything as conspicuous as these features would seem to indicate that they do not occur on S. marginata, X. maculata and X. varia, such a conclusion should not be adopted until the larvae in question have been reexamined. These clear areas may characterize larvae of all species of Solva. If Xylomyia larvae also possess them, the character may prove valid for distinguishing larvae of these two genera from all Stratiomyidae larvae. Differences in number, form and distribution of these areas seem to be valuable in specific identification. It is the most conspicuous and least variable trait found to distinguish larvae of S. bergi from those of S. pallipes.

Mesially, on venters of abdominal segments five and six, larvae of both *S. bergi* and *S. pallipes* have small, oval areas of noticeably lighter integument (fig. 9). While the clear areas on the thorax have no scales and appear quite homogeneous, the abdominal light areas have small, pale integumentary scales.

On the ventral surface, there is a transverse row of small, blunt spicules near the anterior margin of each of the first seven abdominal segments of S. bergi (fig. 9). The venter of each of the first six abdominal segments has a single, continuous row, usually made up of 17-19 spicules. On the seventh segment, the row is interrupted mesially and is composed of only eight or nine minute, poorly developed spicules. On the dorsal surface, abdominal segments two through seven bear rows of larger, fewer spicules near their anterior margins (fig. 1). The dorsum of the seventh abdominal segment usually has 10 or 11 spicules, and each of the others characteristically has 12-14.

Slightly smaller numbers of spicules occur on abdominal segments two through six of S. pallipes. Each has 13-17 on the venter and 8-11 on the dorsum. There is a row of small, rudimentary spicules on the ventral surface of the first abdominal segment. None occur on the seventh abdominal segment.

It is evident that larvae of all species considered here bear these rows of abdominal spicules on one or both surfaces of some abdominal segments. Austen (1899:185) wrote that, while other investigators had reported these structures on S. pallipes, S. marginata and X. varia, they do not occur on the larva which he was then describing, X. maculata. However, Lundbeck (1907:80) pointed out that, "On the anterior margin of some of the ventral segments there is a transverse row of small warts," and Séguy (1926: fig. 222) illustrated these spicules in a ventral view of the X. maculata larva.

Anterior spiracles (fig. 1) are conspicuous on the first body (prothoracic) segment of both S. bergi and S. pallipes. The lateral face view of each spiracular plate shows two oblique slits in the anterior half and what may be a third opening behind them. So many lines appear in so many levels in the posterior half of this spiracular plate that it is very difficult to interpret. The large circular area apparently regarded as a hole by both Malloch (1917: Pl. 48, fig. 9) and Greene (1926: fig. 1:a) is a structure sculptured superficially with fine lines in both S. bergi and S. pallipes. This appears to be a thin, leaf like shield, attached anteriorly near the two oblique slits. A smaller circle, seen in slightly deeper focus within the larger one, may be the rim of a hole, the third opening into the spiracular plate. Still deeper, an inner rim of the heavily

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Fig. 1. Head and first six body segments of empty puparium in dorsal view, with lateral face of anterior spiracle enlarged at right. a., antenna; a. sp., anterior spiracle; c. a., clear areas lacking integumentary scales; e. s., emergence slit; F. 4, area enlarged in Figure 4; i. sp., intermediate spiracles; p. s., pigmented scales; s., spicules. Fig. 2. Head and first two body segments of cleared puparium, with tracheal trunks and posteriorly projecting skeleton of head showing through ventral body wall. c. a., clear areas; t. r., tectorial rods. Fig. 3. Ventral view of last three segments of puparium. *l.*, lips of respiratory chamber; (see area enlarged in Figure 9). Fig. 4. Enlarged lateral margin of first abdominal segment, with dorsal body wall cut away to show main tracheae. b. w., cut edge of body wall; i. sp., intermediate spiracle; l. t., longitudinal tracheal trunk. Fig. 5. Ventral view of eighth abdominal segment, with portion of ventral body wall and ventral lip and ventral wall of respiratory chamber removed. a. pl., anal plate; a. s., anal slit; b. w., cut edge of body wall; d. l., dorsal lip of respiratory chamber; p. sp., posterior spiracle; r. c., dorsal integument of respiratory chamber. Fig. 6. Adult fly and exuviae of larva and pupa, showing how the latter usually remains in emergence slit of puparium. Fig. 7. Empty puparium, viewed with transmitted light. Fig. 8. Lateral view of pupa.

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sclerotized spiracular wall is clearly evident, and behind that the spirally thickened tracheal trunk can be seen running back into the body.

Posterior spiracles (fig. 5) open through the dorsal wall of the respiratory chamber in the last (eighth abdominal) segment. These flared, bell-shaped spiracles have broad, nearly circular rims or peritremes partitioned off by radiating rods into 26-31 equal sections. Grossly, the posterior spiracles and respiratory chamber of *S. pallipes* appear very similar to those of *S. bergi*, but the former have peritremes made up of 32-39 little sections.

The respiratory chamber, walls of which are sparsely supplied with sclerotized scales, opens to the outside by means of a terminal, transverse slit between conspicuous dorsal and ventral lips (fig. 3). When the whole puparium of either S. bergi or S. pallipes is examined with transmitted light, these lips and the area of the respiratory chamber appear darker and quite distinct from the rest of the segment (fig. 7). Several authors (e.g. Brauer, 1883: 23; Malloch, 1917: 342) have pointed out how much this area appears like an additional segment, and two (Townsend, 1893: 164; Lundbeck, 1907: 79) seem actually to have mistaken it for a diminutive twelfth body segment. Brauer, who regarded the species now referred to Solva and Xylomyia as Subula spp., Stratiomyidae, proposed what appears to be a valid key character for distinguishing these larvae from those of all other genera of Stratiomyidae. He wrote (1883:23), "Letzter Ring halbrund, abgestutzt, ... hinten mit deutlich segmentartig abgesetzten Lippen der queren Stigmenspalte." Sharp's character (1909:35), that the orifice of the respiratory chamber is terminal, "looking backwards," is less valuable, since this condition also exists in larvae of the Stratiomyinae.

Intermediate spiracles are not easily seen. Sharp wrote categorically that larvae of this group are amphipneustic, and Austen (1899: 188) emphasized their apparent lack of intermediate spiracles as a means of distinguishing them from larvae of Stratiomyidae. While Lundbeck detected small and indistinct spiracular plates on the first seven abdominal segments (presumably of X. maculata), he wrote (1907: 80), "these spiracles are certainly not in function." Inconspicuous spiracles were found near lateral margins of the metathoracic as well as the first seven abdominal segments of both S. bergi and S. pallipes (fig. 1). Tracheal branches connect these spiracles with the longitudinal tracheal trunks (fig. 4), but

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no experimental evidence of function or lack of function was obtained.

The head of S. bergi is bluntly conical, with small antennae at the anterolateral corners and with bristles distributed as shown (figs. 1, 2). Parts of the cephalic skeleton which protrude back into the thorax are shown in figure 2. Bischoff (1924:5), who treated this group as Stratiomyidae: Subula, mentioned the occurrence of well developed, wholly sclerotized tectorial rods as a character to distinguish the larvae from those of the (other) Stratiomyidae. These structures are well developed and completely sclerotized in both S. bergi and S. pallipes.



Fig. 9. Enlarged left half (approximately) of sixth abdominal segment of puparium in ventral view. br., bristle; l. i., oval area of light integument; p. s., pigmented scale; s., spicule.

The last segment of the S. bergi puparium bears the anus ventrally as a median longitudinal slit, surrounded by short spines or denticles which point in several directions (fig. 5). Malloch (1917: 317) used the conspicuous denticles just anterior to the anal slit to distinguish these larvae from those of the Stratiomyidae. This seems to be a valid character, but it should be noted that the "transverse series of short teeth" is in some species often broken into a median and two lateral portions, the latter extending more obliquely than transversely (fig. 3; Séguy, 1926: fig. 220). Contrasting the number, positions, sizes and directions of denticles illustrated in Figure 3 with those in Figure 5 shows considerable variation in these structures among different specimens of S. bergi. With respect to this character, there is greater similarity between some S. pallipes larvae and Figure 5 than there is between the specimens of S. bergi from which Figures 3 and 5 were drawn.

Each body segment, except the first and the last, of both

S. bergi and S. pallipes bears three pairs of bristles dorsally and three pairs ventrally, well removed from the lateral margins. Some of these (e.g. the most lateral pair on ventral surfaces of abdominal segments) are minute and difficult to find. Most of the marginal bristles of my specimens of S. pallipes are broken off. Those still present correspond approximately in size and position with those of S. bergi.

On the puparium of S. bergi, two bristles occur near each lateral margin of the prothorax, one on each margin of mesothorax and metathorax, and four bristles are found at or near each lateral edge of abdominal segments one through seven (fig. 9; figs. 1-4). Three of these four are attached slightly ventral to the margin, and the posterior one is so short that it does not project beyond the lateral edge. The three that do project shift relative positions somewhat on the various segments. On the anterior abdominal segments, the shortest bristle is anterior to the two long ones, the bases of which are directly above and below one another (fig. 4). On posterior segments, the long ventral bristle is anterior to all others. All of these marginal bristles appear plumose near their tips when magnified 60 diameters or more (fig. 9).

Bristles on the thorax of S. bergi are distributed as shown (figs. 1, 2). Those on the venter of the terminal segment are depicted in fig. 3. Dorsally, this segment has three large tubercles in a transverse row near the anterior margin and bears a single plumose bristle just anterior to each end of the lips of the respiratory chamber.

Description of Pupa

Pupae of all five species considered here emerge partly or completely from the puparia before yielding adult flies. This contrasts with emergence of all reared Stratiomyidae, adults of which escape directly from the puparia, leaving pupal exuviae completely enclosed.

Mature pupa of S. bergi (fig. 8) apparently very similar to that of S. pallipes; covered by a thin, yellow, transparent integument, through which color markings and bristles of enclosed adult are distinctly visible. Length 5.2-6.5 mm.; greatest width of head (to tips of antenna cases) 1.4 mm.; maximum width of thorax (including wing pads) 1.7-1.75 mm.; widest abdominal segments 1.43-1.5 mm. Antenna cases large, pointing laterally, annulated to their tips. Thorax slightly deeper dorsoventrally (1.5 mm.) than long (1.4 mm.). Wing cases usually reaching middle of third abdominal segment; a few extending to its apex. Cases of metathoracic legs reaching approximately to apex of fourth abdominal segment. Prothoracic

spiracles shaped as illustrated (fig. 1–d) by Greene, situated on small elevations on anterolateral margins of thorax. Other thoracic spiracles described by Townsend not apparent on either cleared pupae or pupal exuviae. Abdomen cylindrical, composed of eight segments. First and last segments without bristles; all segments bare on ventral surfaces. Segments 2–7 each with a transverse row of appressed, yellow, spinelike bristles, just posterior to middle of segment, directed posteriorly. Each long bristle surrounded at base by several shorter ones, the whole group attached to a single tubercle. Segments 1–7 with small, slightly elevated spiracles on lateral surfaces anterior to middle of segment⁴. Apex of last segment distinctly bilobed laterally in both sexes.

SUMMARY

Adults of both sexes of *Solva bergi* were taken in nets from September through December, 1944, as they rested on jungle undergrowth near the north coast of Guadalcanal Island.

Two groups of *S. bergi* larvae were collected in April, 1945, associated with dipterous larvae of several other species, in and beneath the moist, fermenting bark of fallen timber. Adults were reared from both collections.

Anatomical features of larvae, puparia and pupae of *S. bergi* are described with the aid of nine figures. To determine which of these features occur also in other species of *Solva*, comparisons were made with larvae and puparia of *S. pallipes*.

Larvae of Solva and Xylomyia differ markedly from those of other Erinnidae, but they resemble Stratiomyidae larvae very closely. Published figures and descriptions of S. marginata, Xylomyia maculata and X. varia larvae were consulted to find valid characters for distinguishing them and the two species examined from all Stratiomyidae larvae. The following traits, all common to S. bergi and S. pallipes and some reported also for other species of Solva and Xylomyia, may prove valuable in identifying immature stages of these two genera.

1. On thoracic segments one and two, larvae of *S. bergi* and *S. pallipes* have conspicuous smooth, clear areas, the number and distribution of which provide an excellent means of distinguishing these two species. These scaleless areas, unfortunately not mentioned by most European

⁴ Lack of elongated respiratory processes which protrude through holes in the puparia may distinguish these pupae from those of the Stratiomyidae which have terrestrial larvae. Although they have escaped the notice of nearly all investigators, tubular respiratory processes such as those which thrust out through puparial integuments of all terrestrial Stratiomyidae reared by the author may occur generally on terrestrial pupae in this family. Protruding dorsolaterally near each spiracle on the first few abdominal segments, these structures would seem to anchor the pupae so effectively as to prevent their emergence.

authors, may either characterize larvae of the genus Solva or help to distinguish Solva and Xylomyia from all Stratiomyidae larvae.

- 2. Transverse rows of small, blunt spicules occur on one or both surfaces of most abdominal segments of S. bergi, S. pallipes, S. marginata, X. varia and X. maculata. Differences in numbers of spicules are useful in specific identification.
- 3. S. bergi and S. pallipes larvae have anterior, posterior and intermediate spiracles similar to those of Stratiomyidae, but the prominent lips of their posterior respiratory chambers are quite distinct. Terminal segments of all known larvae of Solva and Xylomyia have peculiarly interrupted outlines, with the protruding lips of the respratory chamber appearing like an additional segment.
- 4. The cephalic skeletons which extend back into the thorax of *S. bergi* and *S. pallipes* larvae include well developed, wholly sclerotized tectorial rods.
- 5. A transverse series of short denticles (sometimes broken into a median transverse and lateral oblique portions) occurs just anterior to the anal slit on all *Solva* and *Xylomyia* larvae considered here.
- 6. Pupae of all reared species of *Solva* and *Xylomyia* emerge partly or completely from the puparia before the pupal integuments rupture to yield adult flies.
- 7. Pupae of Solva and Xylomyia differ from those of most terrestrial Stratiomyidae in lacking tubular, protruding respiratory processes.

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